# Enantiornithine (Aves) Tarsometatarsi from the Cretaceous Lecho Formation of Northwestern Argentina

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## ABSTRACT

Enantiornithine tarsometatarsi from the Maastrichtian Lecho Formation at the locality of El Brete (northwestern Argentina) are described together with their associated material. Three new species, namely *Yungavolucris brevipedalis*, *Lectavis bretincola*, and *Soroavisaurus australis*, are recognized. *Y. brevipedalis* is distinguished by having a short and broad tarsometatarsus with a pulleylike trochlea of metatarsal II, and equally long metatarsals III and IV with the distal end of the former laterally curved. The long and slender tarsometatarsus of *L. bretincola* is characterized, among other features, for bearing a hypotarsus developed primarily over the metatarsal II. In turn, *S. australis* exhibits a long and narrow fenestra between the proximal halves of metatarsals III and IV, and the plantar surface of the proximal half of

metatarsal II forms a sharp edge (convergent with those of *L. bretincola*).

The relationships among these three species, and their interrelationships with respect to other Late Cretaceous enantiornithine taxa, are explored. A character analysis based on tarsometatarsal features is presented. This analysis supports the hypothesis that *Soroavisaurus australis* is the sister group of a clade formed by *Avisaurus archibaldi* and a new form from the Two Medicine Formation of Montana. This clade is in turn the sister group of *Neuquenornis volans*. These four taxa compose the monophyletic taxon Avisauridae. In the present analysis, the relationships among *Lectavis bretincola*, *Yungavolucris brevipedalis*, and Avisauridae remain unresolved.

## RESUMEN

Se describen los tarsometatarsos, y material asociado, de Enantiornithes del Maastrichtiano de la Formación Lecho en la localidad de El Brete (noroeste de Argentina). Se reconocen y nombran tres

nuevas especies: *Yungavolucris brevipedalis*, *Lectavis bretincola*, y *Soroavisaurus australis*. *Y. brevipedalis* se distingue por poseer un tarsometatarso corto y ancho, la tróclea del metatarso II en forma

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de polea, los metatarsos III y IV de longitud equivalente, y el extremo distal del metatarso III curvado lateralmente. El delgado y largo tarsometatarso de *L. bretincola* se caracteriza, entre otros rasgos, por poseer un hipotarso desarrollado principalmente sobre el metatarso II. A su vez, *S. australis* exhibe una larga y angosta fenestra entre las mitades proximales de los metatarso III y IV, y la superficie plantar de la mitad proximal del metatarso II formando un borde filoso (convergente con aquel de *L. bretincola*).

Se exploran las relaciones filogenéticas entre estas tres especies, y sus relaciones con respecto a otros Enantiornithes del Cretácico tardío. Se presenta un análisis de caracteres basado en caracteres del tarsometatarso. Este análisis sustenta la hipótesis que *Soroavisaurus australis* es el grupo hermano de un clado formado por *Avisaurus archibaldi* y una nueva forma de la Formación Two Medicine de Montana. Este clado es a su vez el grupo hermano de *Neuquenornis volans*. Estos cuatro taxones comprenden el taxón monofilético Avisauridae. El presente análisis no resuelve las relaciones entre *Lectavis bretincola, Yungavolucris brevipedalis* y Avisauridae.

## INTRODUCTION

The Enantiornithes is a Cretaceous group of volant birds originally recognized by Walker (1981) on the basis of the large assemblage of bones from the Maastrichtian Lecho Formation at the locality of El Brete (southern Province of Salta, northwestern Argentina) (fig. 1). In this paper Walker illustrated several bones from El Brete, including the three types of tarsometatarsi here described, and briefly remarked on the peculiar anatomy of the group. After the erection of the Enantiornithes, several authors assigned previously described forms (Martin, 1983) as well as new taxa (Molnar, 1986; Nessov and Jarkov, 1989; Chiappe, 1991a) to this clade. To date, enantiornithine birds are recorded in the Lower Cretaceous of Australia (Molnar, 1986) and Spain (Sanz et al., in press), and the Upper Cretaceous of South America (Walker, 1981; Chiappe, 1991a, 1991b), North America (Martin, 1983; Chiappe, 1992a; Varricchio and Chiappe, in press), and Asia (Martin, 1983; Nessov, 1984; Nessov and Jarkov, 1989). Furthermore, a putative member of this clade was recently discovered in the Lower Cretaceous of China (Zhou et al., 1992).

The discovery of the Enantiornithes strongly influenced subsequent interpretation of early avian evolution. Nevertheless, their most significant evidence, the large assemblage of bones from El Brete, still remains mostly unstudied. Interpretation of the El Brete enantiornithines is complex due to the poor association among the different specimens. Few bones were found in articulation, and no association between hind and fore-limb elements is known (contra Walker, 1981).

In this paper the enantiornithine tarsometatarsi from El Brete, and the material associated with them, are described. Three new species are recognized and their phylogenetic relationships analyzed. The rest of the El Brete collection will be described elsewhere.

### INSTITUTIONAL ABBREVIATIONS

AMNH     American Museum of Natural History
GI           Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar
LH           Universidad Autónoma, Madrid
MACN     Museo Argentino de Ciencias Naturales, Buenos Aires
MOR       Museum of the Rockies, Bozeman
MUCPv   Museo de Ciencias Naturales, Universidad Nacional del Comahue, Neuquén
PU           Princeton University, Princeton
PVL         Fundación-Instituto Miguel Lillo, Tucumán
QM          Queensland Museum, South Brisbane
UCMP      Museum of Paleontology, University of California, Berkeley
YPM        Yale Peabody Museum, New Haven.

### LOCALITY AND GEOLOGICAL SETTING

The material described here was found in a small quarry (approximately 8 m wide) of the middle section of the Lecho Formation in the Estancia El Brete, in the southern tip of the Argentine province of Salta (fig. 1). The Estancia El Brete is located within the dry, forested, hilly landscape of the southern part of the phytogeographic province of the Yunga. The first excavations of this quarry started in 1975, when a crew of the Fundación-Insti-
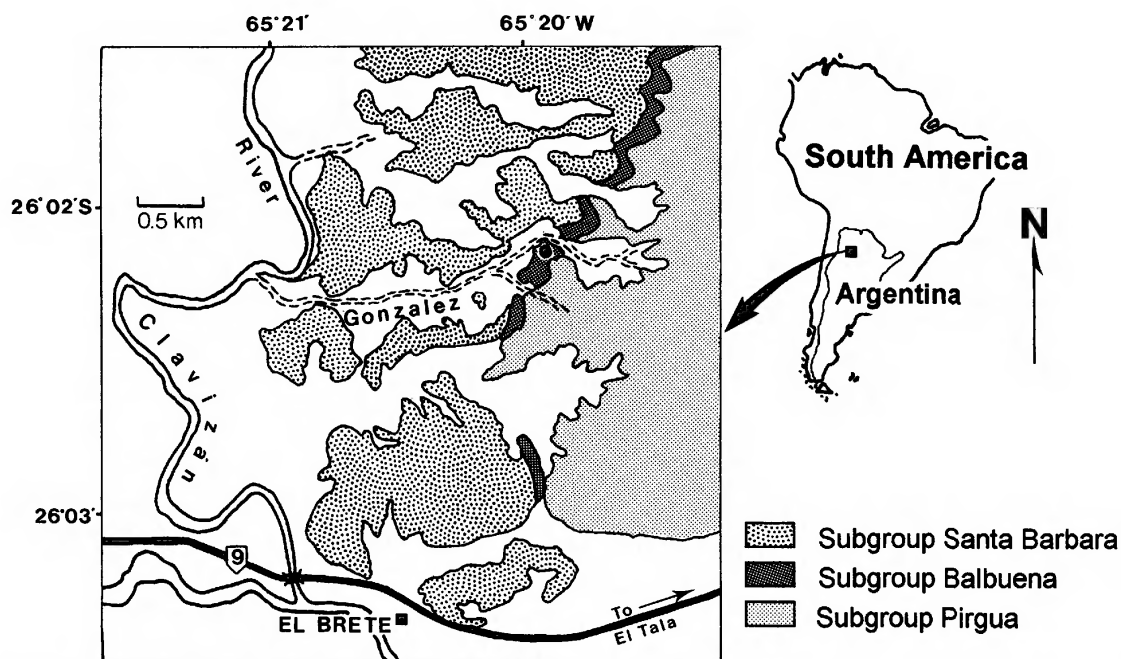
Fig. 1.    Map indicating the locations of the different subgroups of the Salta Group in the lands of the Estancia El Brete and the quarry (black circle) of the Lecho Formation in where the specimens were found. The label "El Brete" shows the farm houses of the Estancia.

tuto Miguel Lillo (Tucumán, Argentina) discovered the fossiliferous locality, which was reported by Bonaparte et al. (1977).

The Lecho Formation is part of the Upper Cretaceous Balbuena Subgroup (Salta Group), a near-border stratigraphical unit of the Andean sedimentary basin (Bonaparte et al., 1977; Bonaparte and Powell, 1980). Recent stratigraphical studies defined the Lecho Formation as those clastic lithofacies of the Balbuena Subgroup deposited in subaerial, fluvial, and eolian environments (Gómez Omil et al., 1989). Lithologically, the Lecho Formation consists of mainly reddish, fine to medium, with an occasional coarse, sandstone (Bonaparte et al., 1977).

The avian assemblage from El Brete comes from fine-grained sandstones. The vertebrate fauna associated with the avian remains is composed of several specimens of the armored titanosaurid *Saltasaurus loricatus,* the small nonavian theropod *Noasaurus leali,* and indeterminate nonavian theropod teeth (Bonaparte and Powell, 1980).

Bonaparte et al. (1977) suggested that the paleoenvironment of the Lecho Formation in the area of El Brete was a fluvial-lacustrine coastal plain, with abundant vegetation and ponds. The age of the Lecho Formation is generally regarded as Maastrichtian on the basis of its fauna (Bonaparte et al., 1977) and stratigraphic relationships (Gómez Omil et al., 1989).

MATERIALS AND METHODS

Anatomical nomenclature follows Baumel et al. (1979), using the English equivalents of the Latin terminology. In regard to the taxonomic names here applied, the term Aves is used in reference to a group including all taxa descended from the most recent common ancestor of *Archaeopteryx lithographica* and modern birds. It is relevant to mention, however, that this application has been recently challenged by new theoretical assertions restricting the name of widely known taxa to the crown group (De Queiroz and Gauthier, 1990, 1992). Under this new interpretation, the taxon name Avialae (Gauthier, 1986) replaces Aves, and the latter substitutes the taxon name Neornithes of the classical avian taxonomy.

The three species erected in this paper are based on incomplete material, which is still

sufficiently diagnostic. It should be noted that these are not the first enantiornithine species named from El Brete. Walker (1981) applied the name *Enantiornis leali* to the specimen PVL-4035 that includes a proximal end of the humerus articulated to the coracoid and scapula. The status of this species name, however, is dubious because Walker (1981) did not describe this specimen and the species name was merely listed in the legend to a table. Because of this, and the additional problems due to the lack of association between forelimb and hind limb elements, this author believes that the tarsometatarsi described in this paper must be allocated in their own species instead of waiting for new material with association of limb elements.

The enantiornithine material studied includes all known tarsometatarsi (and material associated with them) from El Brete (PVL-4021-1, PVL-4040, PVL-4048, PVL-4052, PVL-4053, PVL-4268, PVL-4690, PVL-4692); the enantiornithine tibiotarsi PVL-4030, PVL-4032-1, PVL-4033, PVL-4036, PVL-4695, PVL-4696 from El Brete, and a cast of the holotype (QM F12992) of *Nanantius eos* (Molnar, 1986); the holotype (LH-2814) of *Concornis lacustris* (Sanz and Buscalioni, 1992), recently reinterpreted as an enantiornithine bird (Sanz et al., in press); the holotype (MUCPv-142) of *Neuquenornis volans* (Chiappe and Calvo, in press); a cast (MACN-18685) of the holotype and the paratype PU-17324 (now housed at the YPM) of *Avisaurus archibaldi* (Brett-Surman and Paul, 1985), whose enantiornithine kinship was recently established (Chiappe, 1992a); and the holotype (MOR-553E) of a new avisaurid species from the Two Medicine Formation (Varricchio and Chiappe, in press).

Polarization of character states used in the character analysis was established by using *Patagopteryx deferrariisi* (Alvarenga and Bonaparte, 1992), and *Mononykus olecranus* (Perle et al., 1993a). The Jurassic bird *Archaeopteryx lithographica* was not selected because its two-dimensional preservation obscures several features. The sister-group relationship between Enantiornithes and a clade formed by *P. deferrariisi* plus the Ornithurae has been recently established by this author (Chiappe, 1992b, in press). Under this framework, *P. deferrariisi* is an adequate out-

group for analyzing the enantiornithine interrelationships. *M. olecranus* (see Perle et al., 1993b for nomenclatural correction) has been recently interpreted as the sister group of all known birds except *A. lithographica* (Perle et al., 1993a). The outgroup material studied includes specimens MACN-N-03, MACN-N-10, MACN-N-11, and MUCPv-48 of *P. deferrariisi* (Chiappe, 1992b), and GI N107/6 and GI N100/99 of *M. olecranus* (Perle et al., 1993a).

Derived characters exclusive to a single ingroup taxa were omitted from the analysis in order to avoid their influence on the consistency index (Carpenter, 1988; Wiley et al., 1991). The data matrix presented in table 4 was processed using the implicit enumeration (ie) command of Hennig86 program (Farris, 1988).

## SYSTEMATIC PALEONTOLOGY

### Aves Linnaeus, 1758

### Enantiornithes Walker, 1981

### *Yungavolucris brevipedalis,* new species

DIAGNOSIS: Enantiornithine bird with short and broad tarsometatarsus possessing the following autapomorphies: distal end much broader than proximal end; broad, dorsoplantarly compressed, and pulleylike trochlea of metatarsal II; distal end of metatarsal III laterally curved; metatarsal IV equal in length to metatarsal III; prominent dorsal ridge between distal halves of metatarsals II and III.

ETYMOLOGY: *Yungavolucris* from Latin *volucris,* meaning "bird," and Yunga referring to the phytogeographic region in which El Brete is located; *brevipedalis* from Latin *brevis,* "short," and *pedalis* referring to the foot.

HOLOTYPE: PVL-4053 (fig. 2); nearly complete right tarsometatarsus, lacking the craniolateral border of the lateral cotyla and the cranial portion of the trochlea of metatarsal IV.

REFERRED SPECIMENS: Incomplete right tarsometatarsi PVL-4040 and PVL-4692 (fig. 3), incomplete left tarsometatarsus PVL-4052 (fig. 4), and specimen PVL-4268 represented by the distal trochleae of right metatarsals II and III.

TABLE 1

Measurements (in mm) of *Yungavolucris brevipedalis,* new species

| | PVL specimens | | | | |
|---|---|---|---|---|---|
| | 4040 | 4052 | 4053 | 4268 | 4692 |
| Total length, tarsometatarsus | 41.6 | 51.9 | 41.9 | – | 42.8 |
| Total length, metatarsal II | 37.8 | 41.5 | 37.0 | – | 38.4 |
| Maximum width, proximal end of tarsometatarsus | 16.2 | 15.3 | 14.0 | – | 15.0 |
| Maximum width, trochlea metatarsals II and III | 19.6 | 20.4 | 19.4 | 20.0 | 19.7 |
| Maximum width, trochlea metatarsal II | 11.8 | 10.9 | 10.4 | 12.1 | 11.0 |
| Maximum width, trochlea metatarsal III | 7.2 | 6.8 | 6.2 | 6.3 | 6.5 |

LOCALITY AND HORIZON: 26°02'07"S 65°19'57"W. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina (fig. 1). Lecho Formation, Upper Cretaceous (Maastrichtian).

DESCRIPTION: The tarsometatarsus of *Yungavolucris brevipedalis* is short and stout. It is dorsoplantarly compressed, being generally convex dorsally and flat plantarly (fig. 2). Its distal end is much broader than its proximal end. Metatarsals II, III, and IV are firmly attached to each other, although they are fused only in their proximal portion (figs. 2A, B, 3A).

In the proximal end, the medial cotyla is well developed and suboval; the lateral cotyla is less defined and its articular surface is slightly convex medially (figs. 2E, 3B, 4). Both an intercondylar eminence and hypotarsus are absent.

Metatarsal II is the most robust of the three metatarsals, but not the longest. It is straight throughout its length (figs. 2A, B, 3A). Dorsally, in its middle portion it exhibits a very pronounced ovate-shaped tubercle, with its long axis oriented proximodistally (figs. 2A, C, 3A). This tubercle was tentatively interpreted as the area of attachment of the *M. tibialis cranialis* (Brett-Surman and Paul, 1985; Chiappe, 1992a). The distal half of this metatarsal is fairly compressed dorsoplantarly, especially in its medial portion. In the lateral portion of the distal half, its contact with metatarsal III forms a prominent ridge (figs. 2A, C, D, 3A). The distal end of meta-

tarsal II is very broad. The trochlea of this metatarsal is ample, dorsoplantarly compressed and pulleylike (figs. 2F, 3C). Both rims of the trochlea are bulbous and are separated from each other by a broad central furrow. Just proximal to the medial rim of the trochlea, on the medial margin of the dorsal face, there is a dorsomedial projection (fig. 3A). The degree of development and orientation of this projection varies among the different specimens (cf. figs. 2A, 3A).

Metatarsals III and IV are bent laterally over their distal third, and they are much longer than metatarsal II (figs. 2A, B, 3A). In the dorsal face of the metatarsal III, just distal to the proximal end, there is a slender and elongated ridge for muscle attachment (fig. 2A). Distally, in spite of the lateral bending of the shaft, the trochlea of metatarsal III is in a vertical position (figs. 2A, B, F, 3A, C). The medial rim of this trochlea is larger and more bulbous than the lateral (fig. 3A, B), and deep collateral ligamental fossae excavate both sides.

Metatarsal IV is very small with respect to metatarsals III and II (figs. 2A, B, 3A). It is more weakly attached to metatarsal III than this one is to metatarsal II. The trochlea is missing in all available specimens except in the holotype where only the plantar half is preserved. It is simple and laterally compressed (fig. 2A, B, D, F).

REMARKS: Comparisons between the tarsometatarsi of *Yungavolucris brevipedalis* and those of the remaining enantiornithine taxa

Fig. 2.   Holotype specimen (PVL-4053) of *Yungavolucris brevipedalis,* n. sp. Right tarsometatarsus in dorsal (**A**), plantar (**B**), medial (**C**), lateral (**D**), proximal (**E**), and distal (**F**) views. dp dorsomedial projection of the distal end of metatarsal II, dr distal ridge between the contact of metatarsals II and III, tu tubercle for the attachment of the *M. tibialis cranialis,* lc lateral cotyla, mc medial cotyla, rm elongate proximal ridge for muscle attachment, II–IV metatarsals II–IV.

and the outgroup forms indicate several autapomorphies diagnosing the former taxon.

The remarkable difference between the width of the proximal and distal ends of the tarsometatarsus in *Yungavolucris brevipedalis* is unique to this species among the Enantiornithes (cf. figs. 2A, 7A, 12A). In *Soroavisaurus australis, Avisaurus archibaldi,*

Fig. 2. Continued.

Neuquenornis volans, Concornis lacustris, and the Two Medicine Formation form, the distal end is only slightly broader than the proximal end. This condition is unknown in Lectavis bretincola. In the outgroups, the difference between the width of the proximal and distal
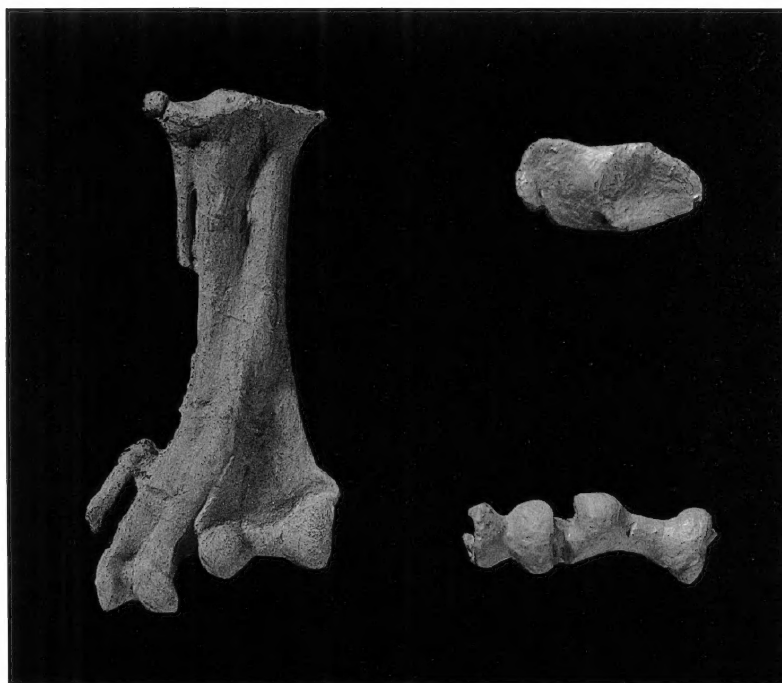
Fig. 3.   Right tarsometatarsus (PVL-4692) of *Yungavolucris brevipedalis,* n. sp. in dorsal (A), proximal (B), and distal (C) views, dp dorsomedial projection of the distal end of metatarsal II, tu tubercle for the attachment of the *M. tibialis cranialis,* lc lateral cotyla, mc medial cotyla, rm elongate proximal ridge for muscle attachment, II–IV metatarsals II–IV.

ends of metatarsals II–IV is also considerably smaller than in *Y. brevipedalis.* The significant difference in the width of the two ends of the tarsometatarsus is autapomorphic for *Y. brevipedalis.*

The tarsometatarsus of *Yungavolucris brevipedalis* differs from all other known enantiornithine tarsometatarsi (the condition is unknown in *Lectavis bretincola*) in that the distal end of metatarsal III curves laterally (figs. 2A, B, 3A), instead of being straight. A straight metatarsal III is also present in the outgroup species *Patagopteryx deferrariisi* and *Mononykus olecranus.* This feature is interpreted as an autapomorphy of *Y. brevipedalis.*

The presence in *Yungavolucris brevipedalis* of a prominent ridge on the distal half of the dorsal surface of the tarsometatarsus between the union of the metatarsals II and III is absent in *Lectavis bretincola* (fig. 6A), *Soroavisaurus australis* (figs. 7A, 8A, 9), *Neuquenornis volans* (fig. 9), *Avisaurus archibaldi* (fig. 12A), *Concornis lacustris,* and the Two Medicine Formation form. The absence of this

feature in the outgroups indicates that it is another autapomorphic character of *Y. brevipedalis.*

In contrast to *Soroavisaurus australis* (figs. 7A, B, 8), *Avisaurus archibaldi* (fig. 12), *Concornis lacustris,* and the Two Medicine Formation form, metatarsal IV of *Yungavolucris brevipedalis* is as long as, not shorter than, metatarsal III (fig. 2A, B). The condition remains unknown in *Neuquenornis volans* and *Lectavis bretincola* in which the distal end of this metatarsal is missing. Metatarsal IV is shorter than metatarsal III in the outgroup forms. The subequal length of metatarsals III and IV is also regarded as an autapomorphy of *Y. brevipedalis.*

The tarsometatarsus of *Yungavolucris brevipedalis* also differs from the tarsometatarsus of *Soroavisaurus australis* (figs. 7F, 11), *Avisaurus archibaldi* (fig. 11), *Neuquenornis volans, Concornis lacustris,* and the Two Medicine Formation form in having a remarkably broad, dorsoplantarly compressed, and pulleylike trochlea of metatarsal II (figs. 2F, 3C). In *Lectavis bretincola* the condition
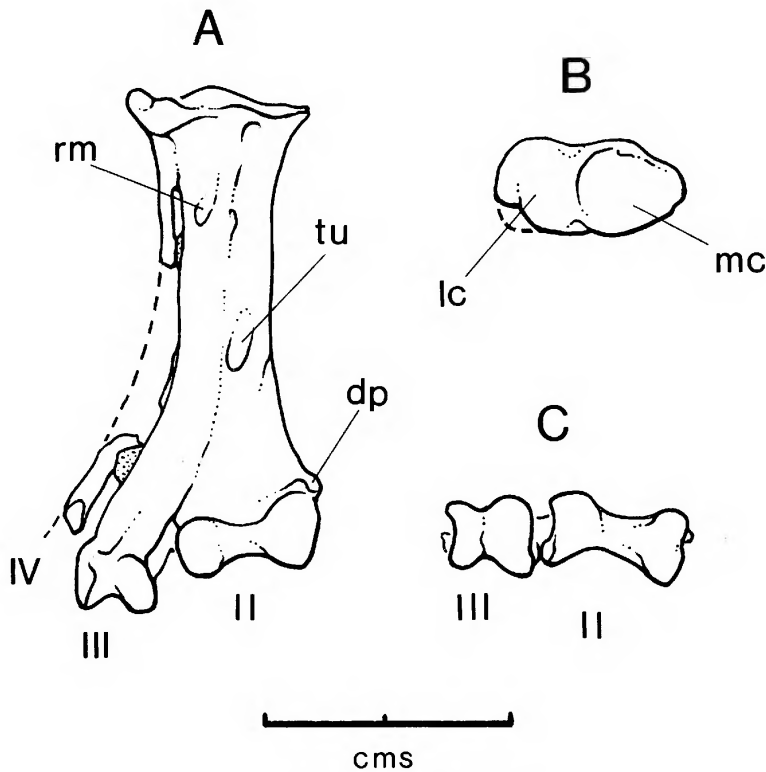
Fig. 3. Continued.

is unknown. This peculiar morphology is also absent in the outgroups, being here interpreted as another autapomorphy of *Y. brevipedalis.*

### Lectavis bretincola, new species

DIAGNOSIS: Enantiornithine bird with long and slender tibiotarsus and tarsometatarsus possessing the following autapomorphies: suboval articular surface of proximal end of tibiotarsus; distal tibiotarsal condyles strongly projected cranially; plantar surface of proximal half of metatarsal II forming a prominent edge; subcircular knob on proximal end of metatarsal II; hypotarsus mostly developed over metatarsal II.

ETYMOLOGY: *Lectavis* from Latin *lectus,* equivalent to the the Spanish word *lecho* ("bed"), in reference to the Lecho Formation,
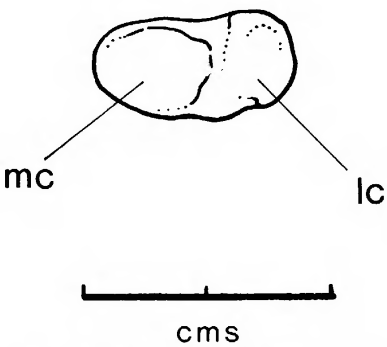


Fig. 4. Left tarsometatarsus (PVL-4052) of *Yungavolucris brevipedalis,* n. sp. in proximal view. lc lateral cotyla, mc medial cotyla.

TABLE 2
Measurements (in mm) of *Lectavis bretincola*, new species

|  | Specimen PVL-4021-1 |
| --- | --- |
| Maximum preserved length, tarsometatarsus | 88.0 |
| Maximum width, proximal end of tarsometatarsus | 15.0 |
| Maximum depth, proximal end of tarsometatarsus | 10.7 |
| Total length, tibiotarsus | 156.0 |
| Maximum depth, mid-shaft of tibiotarsus | 4.8 |
| Maximum width, distal end of tibiotarsus | 14.3 |
| Maximum depth, lateral condyle of tibiotarsus | 12.7 |
| Maximum depth, medial condyle of tibiotarsus | 14.3 |

and *avis*, "bird"; *bretincola* from the combination of "Brete" and the Latin *incola*, which means "an inhabitant."

HOLOTYPE: PVL-4021-1 (figs. 5, 6). Left tibiotarsus and incomplete tarsometatarsus, missing the distal end of the latter and most of metatarsal IV.

LOCALITY AND HORIZON: 26°02'07"S 65°19'57"W. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina (fig. 1). Lecho Formation, Upper Cretaceous (Maastrichtian).

DESCRIPTION: The tibiotarsus of *Lectavis bretincola* is poorly preserved. It is long, slender, and craniocaudally compressed (fig. 5). The morphology of the proximal end differs with respect to the other El Brete enantiornithine tibiae (e. g., PVL-4032-1, PVL-4033, PVL-4036, PVL-4696), *Concornis lacustris* (Sanz and Buscalioni, 1992), and the Australian enantiornithine *Nanantius eos* (Molnar, 1986) in that in proximal view it is not circular but ellipsoidal, with a lateromedial major axis. The shaft is compressed craniocaudally (fig. 5). Distally, the condyles of the tibiotarsus of *L. bretincola* are strongly projected cranially, much more than in any other enantiornithine tibiotarsi from El Brete (e.g., PVL-4030, PVL-4033, PVL-4695) and in *N. eos*. As in the remaining enantiornithines, the medial condyle is inflated, and considerably larger than the lateral one (fig. 5A). The intercondylar notch separating these condyles is less pronounced and broader than in the remaining El Brete tibiotarsi and in *N. eos*. Well-developed epicondylar fossae are present on the sides of the condyles.

*Lectavis bretincola* possesses a long and slender tarsometatarsus (fig. 6). Metatarsals II–IV are strongly attached to each other over their length, and they are completely fused proximally (fig. 6A). The fusion between metatarsals II and III starts more distally (approximately 24.7 mm from the proximal end) than does the fusion between metatarsals III and IV (approximately 17.3 mm from the proximal end). Dorsally, the tarsometatarsus of *L. bretincola* is in general flat, while in plantar view it is deeply excavated (fig. 6B, C). This excavation is especially pronounced in the proximal portion, where metatarsal II forms a strong ridge that medially borders a depressed area formed by metatarsals III and IV (fig. 6B, C).

In dorsal view metatarsal III is the broadest, narrowing smoothly distally. Its proximal portion is dorsoplantarly thin while distally it becomes thicker. Metatarsal II is the more conspicuous of the three. Its main axis is in the dorsoplantar plane, and plantarly it forms a prominent and robust ridge (fig. 6B, C, D), which attenuates distally. In the most proximal portion, this ridge is continuous with a triangular-shaped hypotarsus (fig. 6B). In contrast to the typical modern avian condition, the hypotarsus of *Lectavis bretincola* is mostly developed on the plantar surface of metatarsal II. The medial surface of this metatarsal is basically flat, with only a slightly depressed central area in its most proximal portion (fig. 6D). Dorsally, in the most proximal portion of metatarsal II, there is a prominent round tubercle. Above this tubercle, a nearly crescent-shaped fossa is located between metatarsals II and III (fig. 6A). Metatarsal IV is badly preserved. It is significantly smaller than the remaining ones (fig. 6A, B, C). Its proximal portion is remarkably thin.
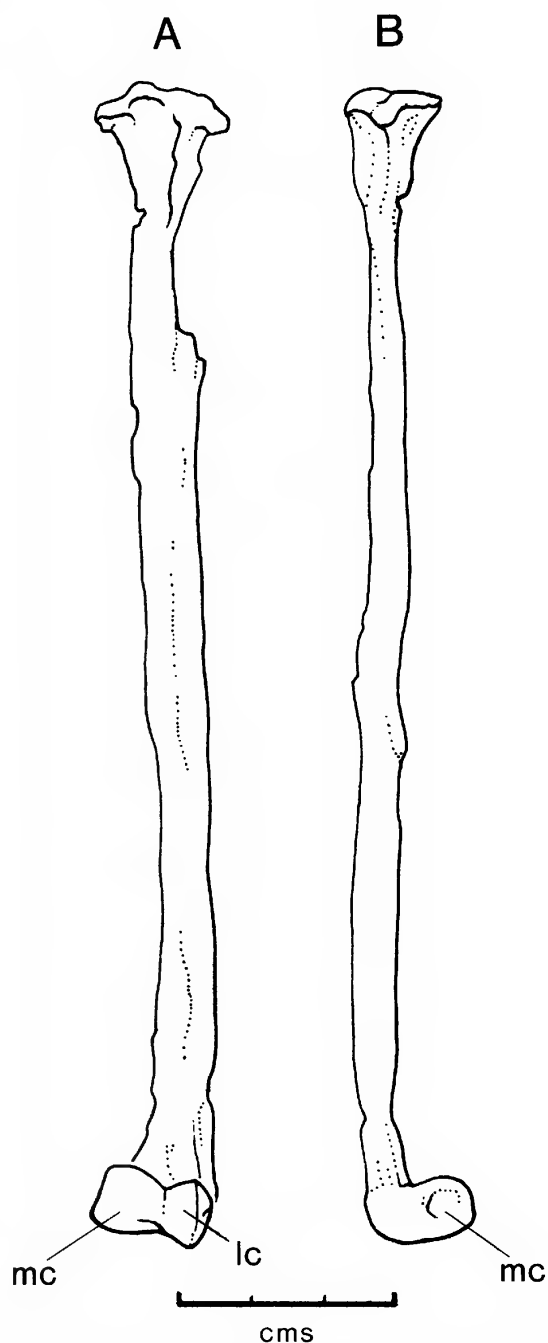
Fig. 5. Holotype specimen (PVL-4021-1) of *Lectavis bretincola,* n. sp. Left tibiotarsus in cranial (**A**), and medial (**B**), views. lc lateral condyle, mc medial condyle.

On the basis of the groove left for its contact on the lateral border of metatarsal III, as with the latter, metatarsal IV became thicker toward the distal end.

Both cotylae in the proximal articular surface are ovate in outline (fig. 6E), and their major axes are oriented in a mediodorsal-lateroplantar direction. The medial cotyla is slightly larger than the lateral cotyla, and its dorsal border is more elevated as well. The plantar border of the medial cotyla, above the hypotarsus, is projected proximally (fig.

Fig. 6. Holotype specimen (PVL-4021-1) of *Lectavis bretincola,* n. sp. Left tarsometatarsus in dorsal (**A**), plantar (**B**), lateral (**C**), medial (**D**), and proximal (**E**) views. tu tubercle for the attachment of the *M. tibialis cranialis,* lc lateral cotyla, mc medial cotyla, II–IV metatarsals II–IV.
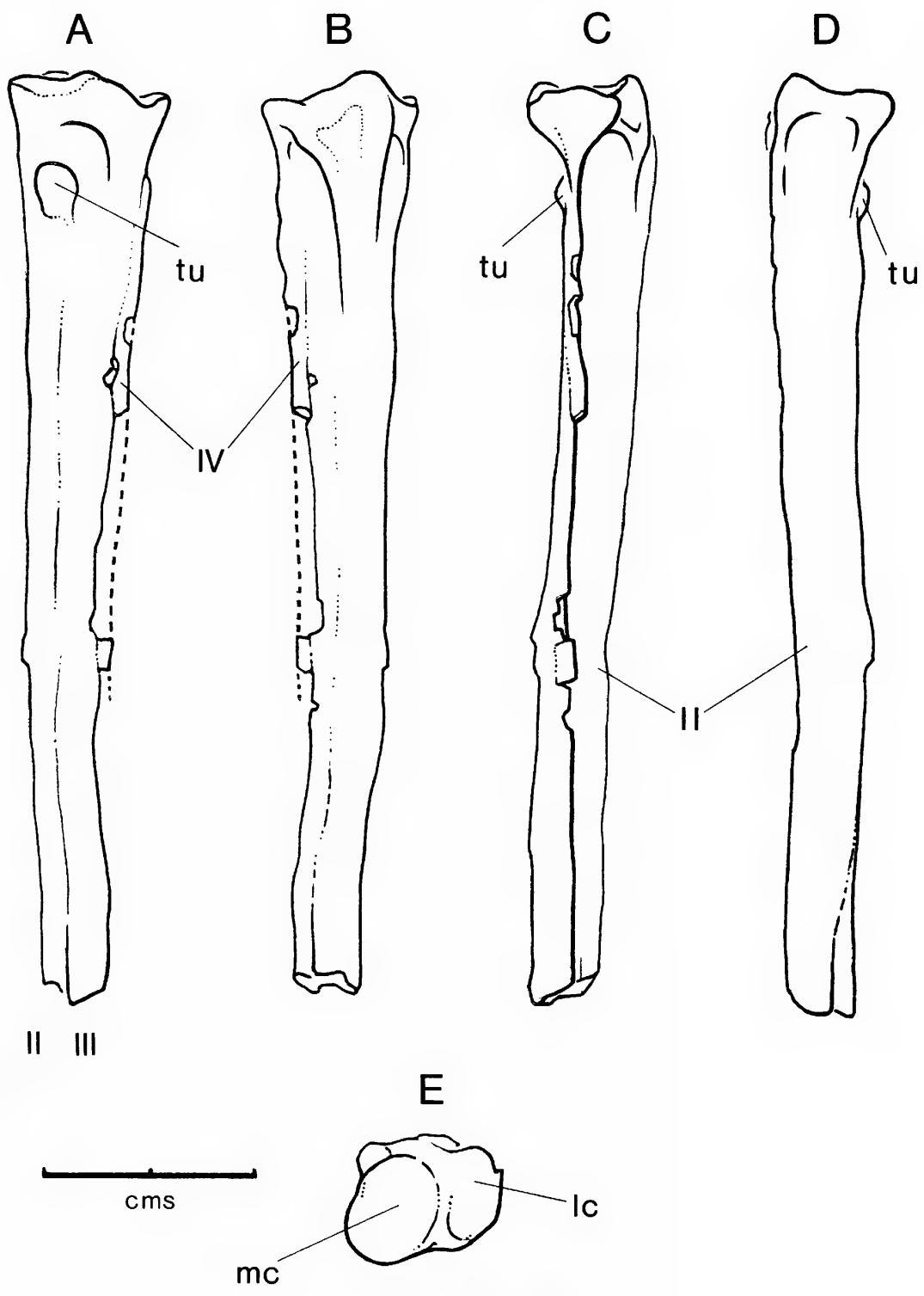
Fig. 6. Continued.

6E). As was pointed out by Walker (1981), the hypotarsus has a subrectangular shape in proximal view, and lacks any crest or sulcus (fig. 6B, E).

The distal end of the tarsometatarsus of the single specimen of *Lectavis bretincola* is missing. With the available material it is not possible to estimate, even roughly, the approximate length of this tarsometatarsus.

REMARKS: Character-state comparisons among *Lectavis bretincola,* the remaining enantiornithines, and the outgroup forms reveal several autapomorphic features of the former species.

In the tibiotarsus, the suboval proximal end and the strong cranial projection of the distal condyles differ from those of the remaining enantiornithines and the outgroups, and are here considered autapomorphies of *Lectavis bretincola.*

In the tarsometatarsus, *Lectavis bretincola* differs from all other enantiornithine taxa in having a hypotarsus (fig. 6B). Contrary to the statements of Brett-Surman and Paul (1985), the tarsometatarsus of *Soroavisaurus australis* (figs. 7B, E, 8B) and *Avisaurus archibaldi* (fig. 12B) lacks a hypotarsus (Chiappe, 1992a), a condition also shared with *Yungavolucris brevipedalis* (figs. 2B, E, 3B, 4), the Two Medicine Formation form, and the outgroup forms. The presence of a hypotarsus in *L. bretincola* is here regarded as an autapomorphy of this taxon. As was mentioned above, the hypotarsus of *L. bretincola* differs from the typical modern avian condition in that it appears to be formed mainly over metatarsal II, instead of capping mostly the proximal end of metatarsal III (Baumel et al., 1979). This indicates that the development of a plantar structure on the proximal end of the tarsometatarsus, a hypotarsus, arose independently in modern birds and certain enantiornithines.

*Lectavis bretincola* differs from other enantiornithines in that the tubercle on metatarsal II is circular instead of ovate as in *Yungavolucris brevipedalis* (figs. 2A, 3A), *Soroavisaurus australis* (figs. 7A, 8A), *Avisaurus archibaldi* (fig. 12A), and the Two Medicine form. The round morphology of this tubercle in *L. bretincola* is interpreted as an autapomorphy.

The tarsometatarsus of *Lectavis bretincola*

is distinct from the tarsometatarsi of *Yungavolucris brevipedalis* (fig. 2B, C), *Neuquenornis volans, Avisaurus archibaldi* (fig. 12B), and the Two Medicine form in that the proximal half forms a robust and laterally compressed medial edge that projects plantarly (fig. 6A, C, D). A medial ridgelike plantar projection is also present in the tarsometatarsus of *Soroavisaurus australis* (figs. 7B, D, 8B). However, this condition differs from the condition present in *L. bretincola* in that the ridge is less robust and more compressed laterally, and in that its most prominent area is not located in the proximal end but more distally (cf. figs. 6D, 7D). Furthermore, in *L. bretincola* the proximal region of this ridge receives the contribution of metatarsal III, whereas it is exclusively formed by metatarsal II in *S. australis*. This prominent plantar ridge is completely absent in the outgroup forms. The important differences between the plantar ridges of the tarsometatarsus of *L. bretincola* and *S. australis* make a hypothesis of homology of these structures unlikely. Hence, the medial plantar ridge of *L. bretincola* is regarded as an autapomorphy.

## AVISAURIDAE BRETT-SURMAN AND PAUL, 1985

DIAGNOSIS: Enantiornithine birds with a strong transverse convexity of the dorsal surface of the mid-shaft of metatarsal III, a distinct plantar projection of the medial rim of the trochlea of metatarsal III, and a laterally compressed J-shaped metatarsal I (see Chiappe, 1992a).

DEFINITION: Phylogenetically defined (see De Queiroz and Gauthier, 1990, 1992) as the common ancestor of *Neuquenornis volans* and *Avisaurus archibaldi* plus all its descendants.

INCLUDED SPECIES: *Avisaurus archibaldi* (Brett-Surman and Paul, 1985), *Neuquenornis volans* (Chiappe and Calvo, in press), *Soroavisaurus australis,* n. sp. (this paper), unnamed new species from the Two Medicine Formation (Varricchio and Chiappe, in press).

### *Soroavisaurus australis,* new species

DIAGNOSIS: Enantiornithine avisaurid with the following autapomorphies: plantar surface of proximal half of metatarsal II forming a sharp edge (convergent with *Lectavis bre-*

*tincola*); long and narrow fenestra open between the proximal halves of metatarsals III and IV; dorsally projected edge on the trochlea for metatarsal IV.

ETYMOLOGY: *Soroavisaurus* from Latin *soror*, meaning "sister," and *Avisaurus* (Brett-Surman and Paul, 1985), referring to the sister-group relationship inferred for these two taxa; *australis* refers to the ocurrence of this species in the Southern Hemisphere.

HOLOTYPE: PVL-4690 (fig. 7), left tarsometatarsus. Specimen previously referred to as *Avisaurus* sp. (Brett-Surman and Paul, 1985; Chiappe, 1992a; Chiappe and Calvo, in press).

REFERRED SPECIMENS: PVL-4048, left tarsometatarsus, metatarsal I with proximal and distal phalanges of digit I, and four intermediate phalanges. This specimen was also formerly identified as *Avisaurus* sp. (Brett-Surman and Paul, 1985; Chiappe, 1992a; Chiappe and Calvo, in press).

LOCALITY AND HORIZON: 26°02'07"S 65°19'57"W. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina (fig. 1). Lecho Formation, Upper Cretaceous (Maastrichtian).

DESCRIPTION: The tarsometatarsus of *Soroavisaurus australis* is gracile (figs. 7, 8). Metatarsals II–IV are fused only proximally (figs. 7A, B, 8), and distally these metatarsals are not as closely apposed as in *Yungavolucris brevipedalis* or *Lectavis bretincola*. The proximal end is transversely much broader than cranioplantarly. The plane of the proximal articular surface is inclined dorsally (fig. 7C, D). In proximal view, the articular surface is kidney-shaped, with the concave part facing plantarly (fig. 7E). In this respect, *S. australis* differs from *Avisaurus archibaldi*, in which the proximal surface is more oval. The medial cotyla is subcircular and of approximately the same size as the lateral one. The articular surface of the latter was a smooth convexity of the medial portion (fig. 7E).

Metatarsal III is the largest. It is straight and dorsally broader than the other two (figs. 7A, 8A). The cranial surface of this metatarsal is convex, especially in the middle of the shaft. Plantarly, this metatarsal constitutes the floor of a depression defined by the plantar projection of the proximal two-thirds of metatarsals II and IV (figs. 7B, 8B). Meta-

TABLE 3
Measurements (in mm) of *Soroavisaurus australis*, new species

|  | PVL-4690 | PVL-4048 |
|---|---|---|
| Total length, tarsometatarsus | 46.9 | 51.5 |
| Maximum width, proximal end of tarsometatarsus | 10.0 | 11.3 |
| Maximum depth, proximal end of tarsometatarsus | 6.3 | 6.1 |
| Total length, metatarsal II | 44.2 | 48.9 |
| Total length, metatarsal IV | 43.3 | 48.4 |
| Maximum width, mid-shaft of tarsometatarsus | 9.9 | 9.6 |
| Maximum width, distal end of tarsometatarsus | 14.6 | 15.2 |
| Maximum width, trochlea metatarsal II | 5.8 | 5.2 |
| Maximum width, trochlea metatarsal III | 4.1 | 4.2 |
| Maximum width, trochlea metatarsal IV | 4.0 | 4.3 |
| Maximum length, metatarsal I | — | 12.2 |

tarsal II is more laterally compressed. The middle portion of its plantar surface forms a prominent edge that limits the medial border of the abovementioned plantar depression (figs. 7B, D, 8B). In *Avisaurus archibaldi*, the plantar border of this metatarsal is slightly projected plantarly, but it does not form this prominent ridge (fig. 12B). In the dorsal surface of the proximal third an oval tubercle is developed. This tubercle is not as prominent as in *A. archibaldi*, and is located more proximally than in the latter species (figs. 7A, 8A). In medial view, the shaft of this metatarsal is slightly sigmoid, as best exhibited by the holotype specimen. Distally, metatarsal II is more widely separated from metatarsal III than the latter is from metatarsal IV (figs. 7A, 8A). Metatarsal IV is weak and dorsoplantarly compressed, especially in its distal half. In its proximal half, it is extremely slender and more bar-shaped, defining the lateral border of an elongate fenestra separating it from metatarsal III (figs. 7A, B, 8). This fenestra is absent in all other enantiornithines.

Distally, the three trochleae are well developed. As in all avisaurids, the trochlea for metatarsal III possesses a remarkable plantar

Fig. 7. Holotype specimen (PVL-4690) of *Soroavisaurus australis,* n. sp. Left tarsometatarsus in dorsal (**A**), plantar (**B**), lateral (**C**), medial (**D**), proximal (**E**), and distal (**F**) views. fe fenestra between metatarsals III and IV, tu tubercle for the attachment of the *M. tibialis cranialis,* lc lateral cotyla, mc medial cotyla, II–IV metatarsals II–IV.
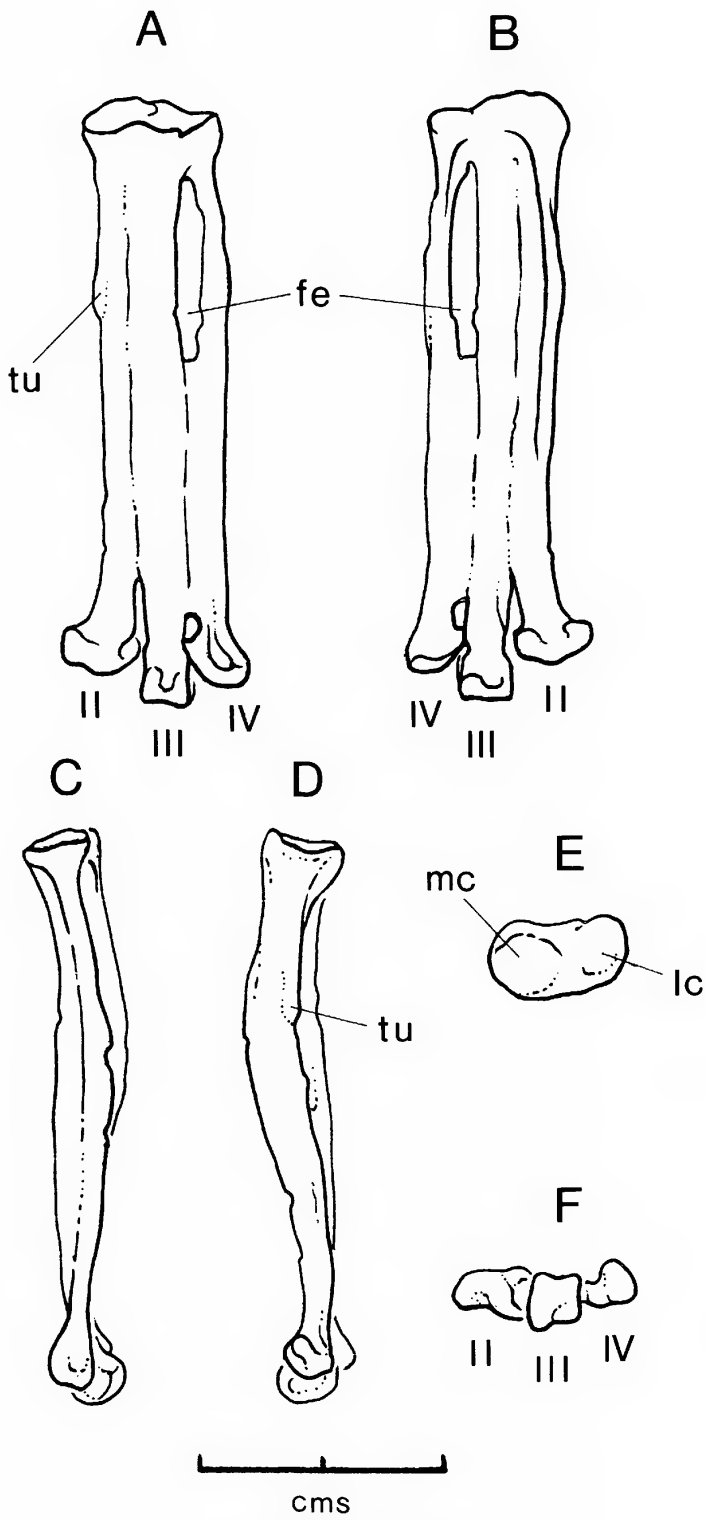
Fig. 7. Continued.

Fig. 8.   Left tarsometatarsus (PVL-4048) of *Soroavisaurus australis,* n. sp. in dorsal (A), and plantar (B) views. fe fenestra between metatarsals III and IV, tu tubercle for the attachment of the *M. tibialis cranialis,* II–IV metatarsals II–IV.

projection of the internal rim (Chiappe, 1992a). Collateral fossae are present on both sides of this trochlea. The trochlea for metatarsal II is the broadest, and plantarly it exhibits lateral and medial prominences separated by a wide depression (figs. 7B, 8B, 11). The trochlea for metatarsal IV of *Soroavisaurus australis* clearly differs from that of *Avisaurus archibaldi* (fig. 11). In *S. australis* this trochlea has a subtriangular outline in distal view, with a medial projection that nearly encloses distally a tiny fenestra between metatarsals III and VI (a structure similar to the distal vascular foramen of Ornithurae) (figs. 7A, B, 8B). Conversely, in *A. archibaldi* this trochlea is crescentic in distal view, with a concave medial side. The small fenestra between metatarsals III and IV in *A. archibaldi* is also enclosed distally by a medial projection of the latter trochlea, but the projection is located much further dorsally than in *S. australis* (fig. 11). Furthermore, the

trochlea of metatarsal II of *S. australis* differs from that of *A. archibaldi* in that it has a stout central edge developed on the dorsal surface that is totally absent in *A. archibaldi* (fig. 11).

The tarsometatarsus of PVL-4048 is associated with metatarsal I and the hallux, and four intermediate phalanges. Unfortunately, this author was not able to find any record of the articulation between these bones; they were disarticulated, although with a single number and within a single box. Comparison with the articulated foot of *Neuquenornis volans* (fig. 9) suggests that they all belong to the same specimen and were probably disarticulated during preparation. Metatarsal I of *Soroavisaurus australis* is J-shaped, as in *N. volans* (fig. 9). It is strongly compressed laterally and tapers proximally. As in *N. volans,* although metatarsal I was not reversed (Fig. 9) the hallux was reverted. The hallux is formed by two large phalanges (fig. 10). The proximal phalanx is dorsoplantarly com-
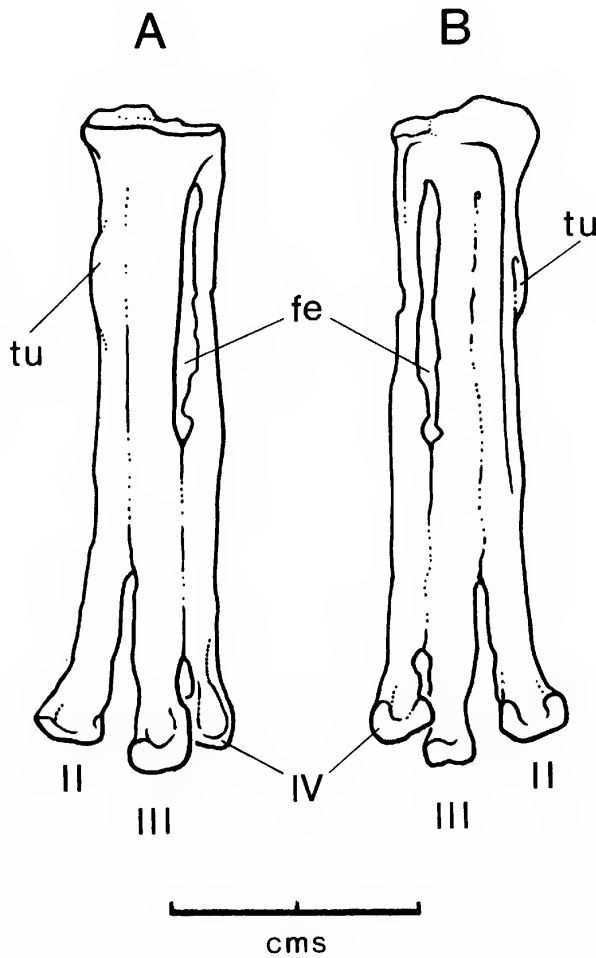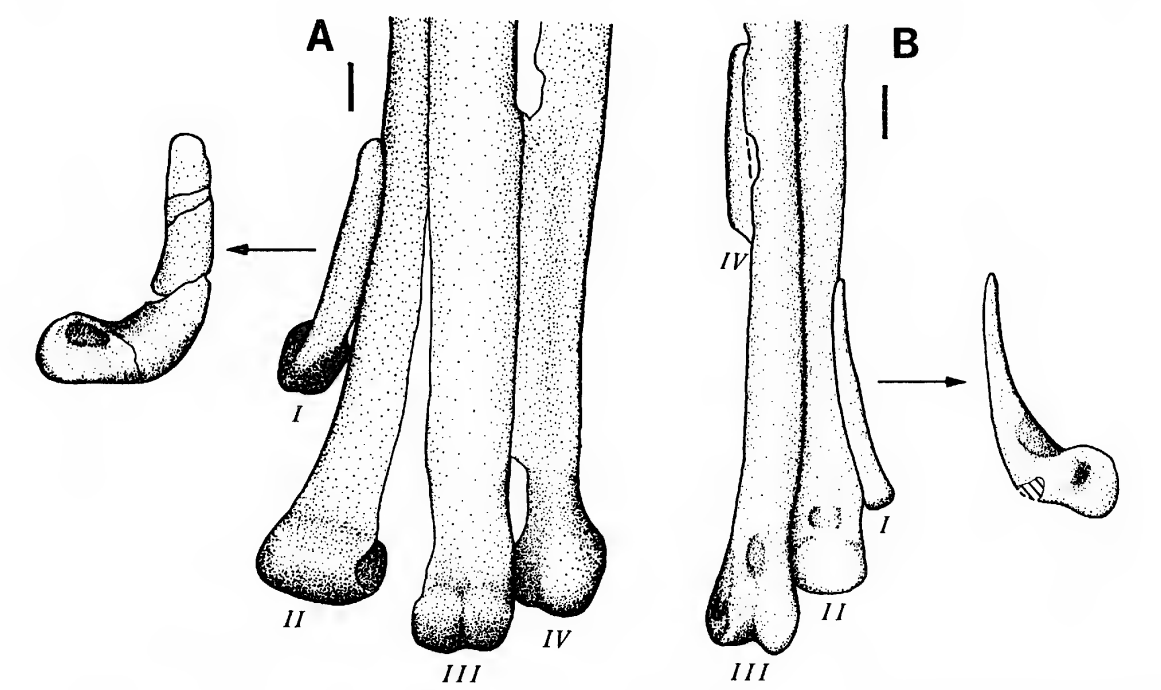
Fig. 8. Continued.

pressed. On its distal head, the articular facet of this phalanx is large and extensively developed on the plantar surface (fig. 10). This suggests that the main movement of the distal phalanx was in a plantar direction. Well-developed collateral fossae are present on both sides of the distal head. The distal phalanx is sharp, laterally compressed, and strongly arched (fig. 10). Plantarly, it possesses a small, round flexor tubercle at its base.

REMARKS: The two known specimens of *Soroavisaurus australis* were previously referred to *Avisaurus* sp. (Brett-Surman and Paul, 1985; Chiappe, 1992a; Chiappe and Calvo, in press). The result of the present cladistic analysis (see below), however, supports their allocation to a different genus.

*Soroavisaurus australis* exhibits several autapomorphic features. The tarsometatarsus differs from the tarsometatarsus of the remaining enantiornithine taxa in the possession of a long and narrow fenestra between the proximal halves of metatarsals III and IV (figs. 7A, B, 8). This fenestra is also absent in outgroup taxa. The presence of a fenestra between metatarsals II and III is here interpreted as an autapomorphy of *S. australis*.

Another autapomorphic character of *Soroavisaurus autralis* is the presence of a stout and thick dorsal trochlear projection of metatarsal IV (figs. 7F, 11). This projection is not developed in either *Avisaurus archibaldi* (fig. 11), *Concornis lacustris,* or the new form from the Two Medicine Formation. In *Yungavolucris brevipedalis* the dorsal portion of the trochlea for the metatarsal IV is missing. However, considering the remarkable reduction of this trochlea (fig. 2), the presence of

*Soroavisaurus australis*                    *Neuquenornis volans*

Fig. 9.  Avisaurid metatarsals I–IV and metatarsal I in dorsal and medial view. (**A**) *Soroavisaurus australis* (based on PVL-4048), (**B**) *Neuquenornis volans* (based on MUCPv-142). Scale bars 2 mm.

a stout dorsal ridge is unlikely. This condition is also uncertain in both *Neuquenornis volans* and *Lectavis bretincola*. A dorsal, thick, central ridge is absent in the trochlea of metatarsal IV in the outgroups.

As was previously discussed (see the Remarks under *Lectavis bretincola*), the presence of a prominent, sharp, and laterally compressed ridge on the plantar surface of metatarsal II of *Soroavisaurus australis* (figs. 7B, D, 8B) is considered an autapomorphy.

### TABLE 4
**Data Matrix of 10 Characters (0 primitive, 1 derived, ? uncertain) of the Tarsometatarsus.**

| | |
|---|---|
| *Mononykus olecranus* | 0000000000 |
| *Patagopteryx deferrariisi* | 0010000000 |
| *Yungavolucris brevipedalis* | 1001??0001 |
| *Lectavis bretincola* | 1?11??00?? |
| *Avisaurus archibaldi* | 1111?11111 |
| *Soroavisaurus australis* | 1111101111 |
| *Neuquenornis volans* | 111?1??101 |
| Two Medicine form | 1101?11111 |

## CHARACTER ANALYSIS

The interrelationships of Enantiornithes are very difficult to evaluate because the El Brete specimens are mostly disarticulated. There is no information about the association between fore- and hind-limb elements, or their association with the pelvis or axial skeleton. This problem is not overcome by the remaining enantiornithine forms recovered in different parts of the world, which are mostly fragmentary or still unpublished. For this reason, this paper presents a tentative approach to the relationships of Late Cretaceous enantiornithines on the basis of the tarsometatarsal morphology alone.

A cladistic analysis of the relationships between the new taxa *Yungavolucris brevipedalis*, *Lectavis bretincola*, *Soroavisaurus australis*, and *Avisaurus archibaldi* (Brett-Surman and Paul, 1985), *Neuquenornis volans* (Chiappe and Calvo, in press), and a new form from the Two Medicine Formation of Montana (Varricchio and Chiappe, in press) was performed. Ten binary characters (table 4) were analyzed cladistically and their dis-
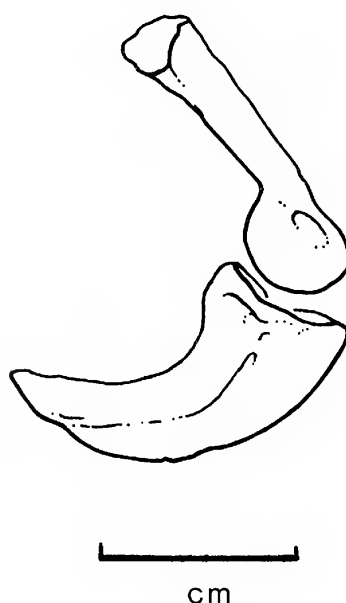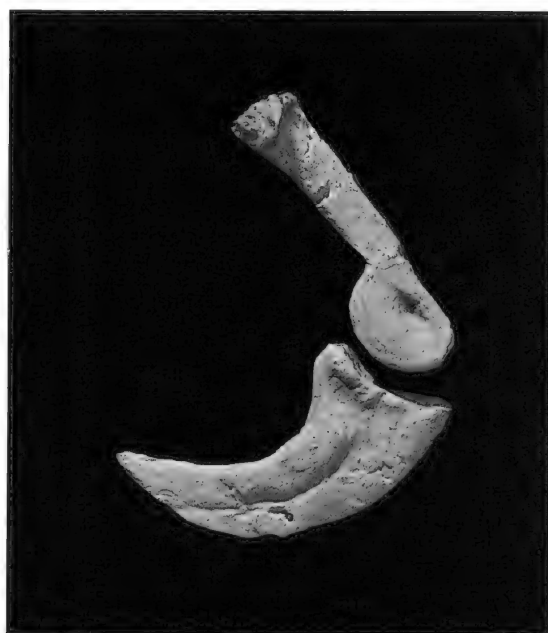
Fig. 10. Digit I of *Soroavisaurus australis* (PVL-4048) in medial view.

tribution among the abovementioned taxa and the outgroups is discussed below.

**1.** Metatarsal IV: large (0) or considerably smaller (1). Metatarsal IV is considerably smaller than metatarsals II and III in all enantiornithine taxa considered in the analysis (figs. 2, 3, 6–8, 12; see also Walker, 1981; Chiappe, 1991a, 1992a). Variable sizes of metatarsal IV are present among the different taxa (cf. figs. 2A, 6A, 7A, 12A), although these differences are not clear enough for scoring distinct character states. This enantiornithine condition is absent in both *Patagopteryx deferrariisi* and *Mononykus olecranus*.

**2.** Medial rim of the trochlea of metatarsal III with a strong plantar projection: absent (0) or present (1). The medial rim of the trochlea of metatarsal III is projected strongly plantarly in *Soroavisaurus australis* (figs. 7F, 11), *Avisaurus archibaldi* (fig. 11), *Neuquenornis volans* (Chiappe and Calvo, in press), and the Two Medicine Formation form (Varricchio and Chiappe, in press). On the other hand, this strong projection is absent in *Yungavolucris brevipedalis* (figs. 2F, 3C) and the outgroups.

**3.** Plantar surface of tarsometatarsus excavated: absent (0) or present (1). In *Lectavis*



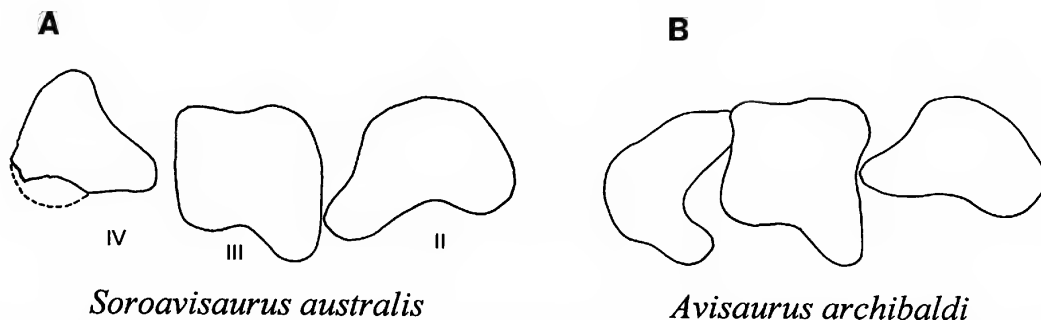*Soroavisaurus australis*                    *Avisaurus archibaldi*

Fig. 11. Comparisons between the distal end of the tarsometatarsus of *Soroavisaurus australis* (PVL-4690) and *Avisaurus archibaldi* (cast MACN-18685). II–IV metatarsals II–IV.

Fig. 12.    Cast (MACN-18685) of the right tarsometatarsus (holotype specimen) of *Avisaurus archibaldi* (Brett-Surman and Paul, 1985) in dorsal (**A**) and plantar (**B**) views. tu tubercle for the attachment of the *M. tibialis cranialis,* II–IV metatarsals II–IV.

*bretincola* (fig. 6B, C), *Soroavisaurus australis* (figs. 7B, 8B), *Avisaurus archibaldi* (fig. 12B), and *Neuquenornis volans* (Chiappe and Calvo, in press) the plantar face of the tarsometatarsus is excavated to variable degrees exhibiting a proximodistal fossa bounded by metatarsals II and IV, giving a crescentic cross section to the tarsometatarsus. Within the remaining enantiornithine taxa considered here, this fossa is absent in *Yungavolucris brevipedalis* (fig. 2B) and the new form from the Two Medicine Formation (Varricchio and Chiappe, in press). Within the outgroup, this fossa is absent in *Mononykus olecranus,* but the tarsometatarsus of *Patagopteryx deferrariisi* is excavated plantarly.

    **4.** Tubercle on the dorsal face of metatar-

sal II: absent (0) or present (1). The dorsal faces of metatarsal II of *Yungavolucris brevipedalis, Lectavis bretincola, Soroavisaurus australis, Avisaurus archibaldi,* and the Two Medicine Formation form exhibit a pronounced tubercle (figs. 2A, 3A, 6A, 7A, 8A, 12A), previously interpreted as the area of attachment of the *M. tibialis cranialis* (Brett-Surman and Paul, 1985). Variable positions of this tubercle occur among the abovementioned forms. The presence or absence of this tubercle is uncertain in *Neuquenornis volans,* in which the proximal half of the shaft of metatarsal II is missing (Chiappe and Calvo, in press). A tubercle on the dorsal surface of metatarsal II is absent in the outgroups.

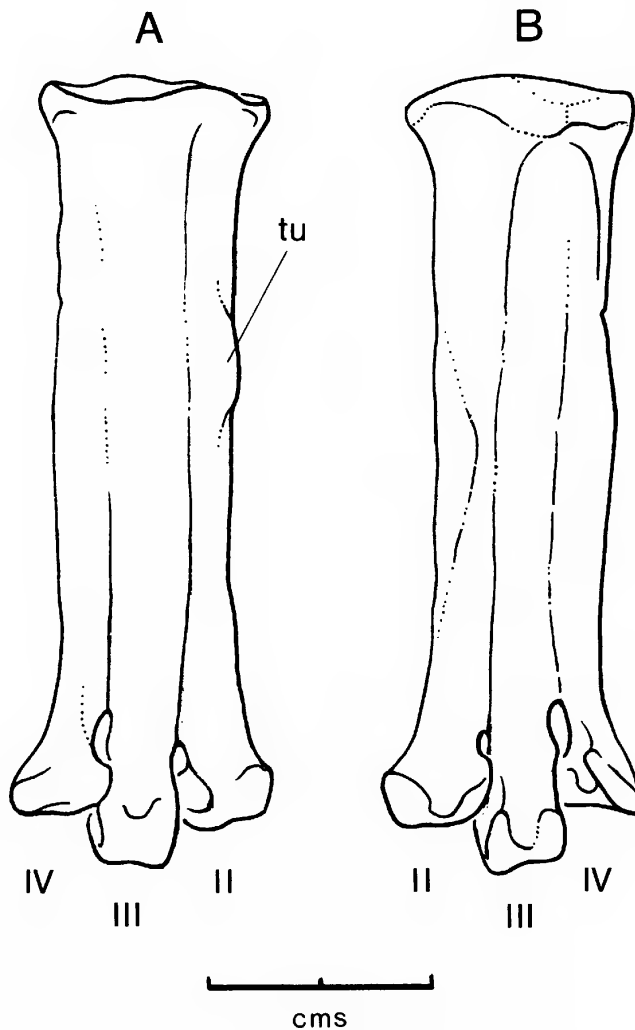    **5.** J-shaped metatarsal I: absent (0) or

Fig. 12.   Continued.

present (1). Metatarsal I of *Soroavisaurus australis* and *Neuquenornis volans* is J-shaped in medial view (fig. 9), and extremely laterally compressed. Unfortunately, metatarsal I is missing in *Yungavolucris brevipedalis, Lectavis bretincola, Avisaurus archibaldi,* and the Two Medicine enantiornithine. This metatarsal morphology is also absent in the outgroups, in which metatarsal I is straight or slightly curved as in *Patagopteryx deferrariisi,* and *Mononykus olecranus.*

6. Trochlea of metatarsal IV medially concave: absent (0) or present (1). In *Avisaurus archibaldi* the trochlea for metatarsal IV is remarkably concave medially, being highly asymmetrical (figs. 11, 12B). In the Two Medicine form, the trochlea for metatarsal

IV is also concave medially and asymmetrical, although to a lesser extent than in *A. archibaldi* (Varricchio and Chiappe, in press). This trochlear morphology is absent in *Soroavisaurus australis* (Fig. 11), while the condition is uncertain in *Yungavolucris brevipedalis, Lectavis bretincola,* and *Neuquenornis volans.* This condition is also absent in the outgroup taxa.

7. Proximal articular surface dorsally inclined: absent (0) or present (1). The articular surface of the proximal end of *Soroavisaurus australis* (fig. 7C, D), *Avisaurus archibaldi* (fig. 12A; see also Brett-Surman and Paul, 1985; fig. 3C, E), and the Two Medicine Formation form (Varricchio and Chiappe, in press) slants toward the dorsal border such that this plane
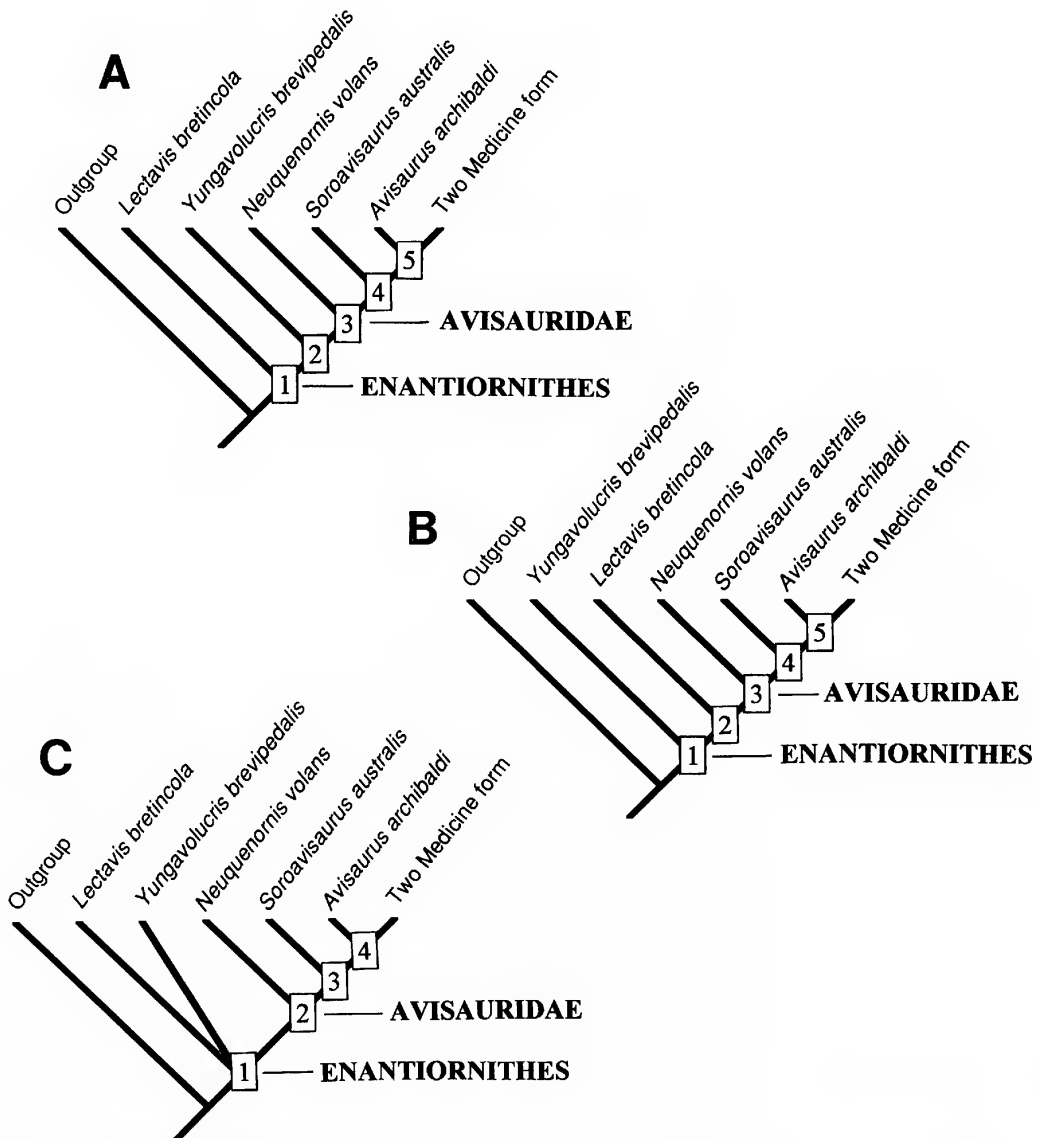
Fig. 13. Fundamental cladograms (length 12, consistency index 0.83, retention index 0.87) resulting from the analysis of the data matrix by using the implicit enumeration option of Hennig86 program. A, node 1: characters 1, 4; node 2: character 10*; node 3: characters 2, 5*, 8; node 4: characters 7*, 9; node 5: character 6. B, node 1: characters 1, 4, 10; node 2: character 3*; node 3: characters 2*, 5*, 8; node 4: characters 7*, 9; node 5: character 6. C, node 1: characters 1, 4, 10; node 2: characters 2, 5*, 8; node 3: characters 7*, 9; node 4: character 6. Asterisked characters have an ambiguous optimization.

forms a sharp angle relative to the dorsal plane of the tarsometatarsus. This character is uncertain in *Neuquenornis volans*. Otherwise, the articular surface of the proximal end is not inclined in *Yungavolucris brevipedalis* (fig. 2C, D), *Lectavis bretincola* (fig. 6C, D), or in any of the outgroup forms.

**8.** Strong transverse convexity of the dorsal surface of the mid-shaft of metatarsal III: absent (0) or present (1). The dorsal surface of the mid-shaft of metatarsal III is strongly convex transversely in *Soroavisaurus australis* (figs. 7A, C, 8A), *Avisaurus archibaldi* (fig. 12A; see also Brett-Surman and Paul,

1985; fig. 3H), *Neuquenornis volans* (Chiappe and Calvo, in press), and the Two Medicine Formation enantiornithine (Varricchio and Chiappe, in press). Conversely, this condition is absent in *Yungavolucris brevipedalis* (figs. 2A, 3A) and *Lectavis bretincola* (fig. 6A). This condition is also absent in the outgroup forms in which the dorsal surface of the midshaft is instead slightly convex or nearly flat.

**9.** Distal end of metatarsal II strongly curved medially: absent (0) or present (1). In *Soroavisaurus australis* (figs. 7A, B, 8), *Avisaurus archibaldi* (fig. 12), and the Two Medicine enantiornithine (Varricchio and Chiappe, in press), the distal end of metatarsal II is strongly twisted medially. This condition is absent in *Yungavolucris brevipedalis* (figs. 2A, B, 3A) and *Neuquenornis volans* (fig. 9). In *Lectavis bretincola* the condition remains unknown. The distal end of metatarsal II is not curved medially in *Patagopteryx deferrariisi* and *Mononykus olecranus*.

**10.** Trochlea of metatarsal II broader than the trochleae of metatarsal III and IV: absent (0) or present (1). In *Yungavolucris brevipedalis* (figs. 2A, B, F, 3A, C), *Soroavisaurus australis* (figs. 7A, B, F, 11), *Avisaurus archibaldi* (figs. 11, 12B), *Neuquenornis volans* (Chiappe and Calvo, in press), and the Two Medicine Formation form (Varricchio and Chiappe, in press) the trochlea of metatarsal II is the broadest trochlea of the tarsometatarsus. This condition is uncertain in *Lectavis bretincola*. Otherwise, the trochlea of metatarsal II is not broader than the trochlea of metatarsal III in *Patagopteryx deferrariisi* and *Mononykus olecranus*.

## PHYLOGENETIC DISCUSSION

Three most parsimonious cladograms (length 12, consistency index 0.83, retention index 0.87) resulted from the cladistic analysis of tarsometatarsal characters (fig. 13). These three fundamental cladograms differ in depicting the relationships among *Lectavis bretincola*, *Yungavolucris brevipedalis*, and the Avisauridae, a group composed of *Neuquenornis volans*, *Soroavisaurus australis*, *Avisaurus archibaldi*, and the Two Medicine Formation form. In two of these cladograms (fig. 13A, B), *L. bretincola* and *Y. brevipedalis*

are successive sister taxa of Avisauridae, although their sequence is reversed. The remaining tree (fig. 13C), identical to the strict consensus, depicts these three taxa clustered in an unresolved tricotomy.

The Enantiornithes, the clade composed of all ingroup taxa, is unambiguously diagnosed by a small metatarsal IV (character 1), a tubercle in the dorsal face of metatarsal II (character 4), and a trochlea of metatarsal II broader than the trochleae of metatarsals III and IV (character 10). In the fundamental cladogram of figure 13A, the latter character supports ambiguously the sister-group relationship between *Yungavolucris brevipedalis* and Avisauridae. On the other hand, the sister-group relationship of the latter taxon and *Lectavis bretincola*, resulting in the fundamental cladogram of figure 13B, is supported ambiguously by the excavated plantar surface of the tarsometatarsus (character 3). The absence of the latter character is optimized as autapomorphic of both *Y. brevipedalis* and the Two Medicine Formation form in the remaining trees (fig. 13A, C).

*Neuquenornis volans*, *soroavisaurus australis*, *Avisaurus archibaldi*, and the Two Medicine enantiornithine are clustered in the monophyletic Avisauridae in all resultant cladograms (fig. 13). The monophyly of the Avisauridae is supported unambiguously by the presence of a strong plantar projection of the medial rim of the trochlea of metatarsal III (character 2), and the transverse convexity of the dorsal surface of the mid-shaft of metatarsal III (character 8) in the cladograms of figure 13A and C. Character 2 has an ambiguous optimization in the remaining cladogram (fig. 13B) in which, pending determination of the condition in *Lectavis bretincola*, it may diagnose a more inclusive clade. In addition, the presence of a J-shaped metatarsal I (character 5) is an ambiguous synapomorphy of Avisauridae in all the resultant cladograms (fig. 13). Pending determination of the condition in *L. bretincola* and *Y. brevipedalis*, the latter character may represent a more inclusive synapomorphy.

Within the Avisauridae, *Neuquenornis volans* is the sister group of the clade composed by *Soroavisaurus australis*, *Avisaurus archibaldi*, and the Two Medicine Formation form (fig. 13). In all resultant cladograms, the latter

three taxa are united by one unambiguous synapomorphy: the strong medial curvature of the distal end of metatarsal II (character 9). In addition, this clade is supported ambiguously by another synapomorphy: the possession of a dorsally inclined proximal articular surface (character 7). Pending determination in *N. volans,* this character may be a synapomorphy of Avisauridae. *S. australis,* in turn, is the sister taxon of the clade formed by *A. archibaldi* and the unnamed form from the Two Medicine Formation (fig. 13). The latter clade is unambiguously diagnosed by the possession of a medially concave trochlea of metatarsal IV (character 5).

## CONCLUSIONS

*Yungavolucris brevipedalis, Lectavis bretincola,* and *Soroavisaurus australis* are three diagnosable taxa possessing synapomorphies that cluster them in the monophyletic Enantiornithes. The recognition of these three new enantiornithine species, in addition to a worldwide distribution (see above), emphasizes the important role played by this group in the Late Cretaceous avifauna.

The proposed phylogenetic hypothesis is the first attempt to understand the interrelationships of the Late Cretaceous enantiornithines. This hypothesis clearly indicates the nonmonophyletic status of the enantiornithine assemblage of El Brete, with some elements (e.g., *Soroavisaurus australis*) sharing a most recent common ancestor with North American taxa. It also supports the monophyly of the Avisauridae, establishing the sis-ter-group relationship of the only two known North American avisaurids (*Avisaurus archibaldi* and the Two Medicine Formation form). It finally corroborates previous claims about the avian affinity of *Avisaurus archibaldi* (Martin 1991; Chiappe, 1992a), a taxon that was originally regarded as a nonavian theropod (Brett-Surman and Paul, 1985; Norman, 1990).

## ACKNOWLEDGMENTS

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